Phylogenetic relationships of *Cyclopsetta* and *Syacium* (Pleuronectiformes: Paralichthyidae)

by

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ABSTRACT. - Phylogenetic relationships among four species of *Cyclopsetta* and eight species of *Syacium* were established based on a total of 29 morphological, meristic and osteological characters (CI = 0.75); *Citharichthys* and *Etropus* were designated as the outgroups. The *Cyclopsetta-Syacium* clade was supported by six synapomorphies. *Cyclopsetta* was strongly supported as monophyletic by ten synapomorphies. This genus was divided into two subgenera, *Cyclopsetta* comprising *C. chittendeni* and *C. fimbriata* and *Azevia* comprising *C. panamensis* and *C. querna*. *Syacium* was also determined to be monophyletic based on five synapomorphies. *S. longidorsale* was the first extant species to evolve followed subsequently by *S. ovale, S. gunteri, S. maculiferum* and a trichotomy containing *S. guineensis, S. micrurum* and the sister species *S. latifrons* and *S. papillosum*.

RÉSUMÉ. - Relations phylogénétiques de *Cyclopsetta* et *Syacium* (Pleuronectiformes : Paralichthyidae).

Notre examen des relations phylogénétiques entre les quatre espèces de *Cyclopsetta* et les huit espèces de *Syacium* se fonde sur l'étude de 29 caractères morphologiques, méristiques et ostéologiques (IC = 0.75) ; *Citharichthys* et *Etropus* ont été utilisés comme extra-groupes. Le clade *Cyclopsetta-Syacium* est soutenu par six synapomorphies. La monophylie de *Cyclopsetta* est fortement soutenue par dix synapomorphies. Nous proposons une division du genre en deux sous-genres, *Cyclopsetta* comprenant *C. chittendeni* et *C. fimbriata* et *Azevia* comprenant *C. panamensis* et *C. querna*. La monophylie de *Syacium* est soutenue, quant à elle, par cinq synapomorphies. *S. longidorsale* est la première espèce actuelle à évoluer, suivie dans l'ordre par *S. ovale, S. gunteri, S. maculiferum* et une trichotomie comprenant *S. guineensis, S. micrurum* et les espèces-sœurs *S. latifrons* et *S. papillosum*.

Key words. - Paralichthyidae - *Cyclopsetta* - *Syacium* - *Citharichthys* - *Etropus* - Cladogram - Phylogeny.

Cyclopsetta Gill, 1889 and *Syacium* Ranzani, 1842 belong to the family Paralichthyidae, an ill-defined group of sinistral flatfishes in need of taxonomic and phylogenetic studies (Hensley and Ahlstrom, 1984). These two genera inhabit the continental shelves of the Atlantic and Pacific coasts of North and South America. *Cyclopsetta* was revised by Khidir *et al*. (2004) and comprises four species: *C. chittendeni* and *C. fimbriata* are found on the Atlantic coast from North Carolina, USA, to Rio de Janeiro, Brazil, and *C. panamensis* and *C. querna* are found on the Pacific coast from Baja California, Mexico to Peru.

Syacium was revised by Murakami and Amaoka (1992) and comprises eight species: Three (*S. gunteri, S. micrurum* and *S. papillosum*) inhabit the Atlantic coast from South Carolina, USA, to Rio de Janeiro, Brazil including the Gulf of Mexico and the Caribbean Sea; and four species (*S. longidorsale, S. latifrons, S. maculiferum* and *S. ovale*) are found along the Pacific coast from Baja California, Mexico to Ecuador. One species, *S. guineensis*, inhabits the Atlantic coast of tropical Africa from the Western Sahara to Angola.

Jordan and Goss (1889) placed *Syacium, Citharichthys, Etropus* and *Azevia* in the subfamily Pleuronectinae of the Pleuronectidae. Jordan and Evermann (1898) added *Cyclopsetta* to these four genera and placed them in the subfamily Psettinae within the Pleuronectidae. Norman (1934) reviewed these five genera (synonymizing *Azevia* with *Cyclopsetta*) and noted that they were closely related, in particular, *Citharichthys* and *Etropus*. He placed his four genera in the subfamily Paralichthyinae, family Bothidae. Hensley and Ahlstrom (1984) defined *Cyclopsetta, Syacium, Citharichthys* and *Etropus* as a monophyletic group and placed them within the family Paralichthyidae. The monophyly was based on six synapomorphies: urinary papilla on the blind side; base of ocular-side pelvic fin on mid-ventral line of the body; base of the blind-side pelvic fin on the blind side and slightly in advance of the ocular side fin; 17 caudal fin rays; these caudal rays not supported by pleural, neural or haemal spines; and the fifth hypural was fused to an epural. Moreover, Ahlstrom *et al*. (1984) divided the four genera into two pairs, *Citharichthys-Etropus* and *Cyclopsetta-Syacium* based

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Cybium 2005, 29(4): 321-326.

on the following three respective larval characters: 2-3 *vs.* 5-11 elongated dorsal fin rays on the crest of head; 0-2 *vs.* 3-6 elongated left pelvic fin rays; and small *vs.* large preopercular spines.

Berendzen and Dimmick (2002) conducted a phylogenetic study of the Pleuronectiformes based on mtDNA evidence from 43 species representing 11 of the 12 families of flatfishes resolved by Cooper and Chapleau (1998). Included in the analysis were *Citharichthys xanthostigma*, *Etropus microstomus* and *Syacium papillosum*. Their results confirmed that *Citharichthys, Etropus* and *Syacium* formed a monophyletic group, as proposed by Hensley and Ahlstrom (1984), and that *Citharichthys-Etropus* constituted a clade, as proposed by Ahlstrom *et al.* (1984) and suggested by Norman (1934). They did not, however, have material for the genus *Cyclopsetta*. The purpose of this study is to test the monophyly of the *Cyclopsetta-Syacium* clade, the monophyly of each genus and to determine the intrarelationships of each genus.

MATERIALS AND METHODS

The phylogenetic analysis was based on 29 morphological, meristic and osteological characters (Appendix) of 14 terminal taxa. Autapomorphies were excluded from the character matrix. All morphological characters were observed on the ocular side except for character 13 (origin of first dorsal ray relative to blind side nostrils), which was observed on the blind side. Larval characters were taken from Ahlstrom *et al.* (1984). For *Syacium*, information about the following characters were taken from Murakami and Amaoka (1992): one or two dark lines from the anterior margin of the upper eye to tip of snout in mature males (4), width of interorbital space in mature males relative to that in females (7), first one or two pectoral fin rays extended and filamentous in mature males (15), dark bars on pectoral fin (16), ocelli on dorsal and anal fins (17), number of caudal vertebrae (23), number of pectoral fin rays (24) and number of lateral line scales (25).

States of characters 23 and 25 of *Etropus crossotus* were taken from Leslie and Stewart (1986). Otherwise, information about the characters was obtained from whole preserved specimens, radiographs and cleared and stained material. Cleared and stained (c&s) specimens were prepared according to Taylor and Van Dyke (1985). Terminology of bones follows Cooper and Chapleau (1998). Institutional abbreviations follow Eschmeyer (1998). SL is standard length in mm (Hubbs and Lagler, 1958).

Table I. - Character states of *Cyclopsetta* and *Syacium* species. *Citharichthys* (*C. gilberti* and *C. stigmaeus*) and *Etropus crossotus* are outgroups. (?) = unknown state. List of characters is in Appendix. *[États des caractères des espèces de* Cyclopsetta *et* Syacium. Citharichthys *(*C. gilberti *et* C. stigmaeus*) et* Etropus crossotus *sont les extra groupes. (?) = état de caractère inconnu. La liste des caractères est en annexe.]*

	Character		
Taxon	1-10	11-20	21-29
Citharichthys	0 (0,2) 00010110	0(0,1)(0,1)0000000	00 (0,1) 000000
Etropus crossotus	1 0 0 0 0 0 0 0 0 2	0 0 0 0 0 0 0 0 ? ?	? 1 0 0 0 0 0 0 0
Cyclopsetta chittendeni	1 0 1 0 0 ? 0 1 1 1	2 1 2 1 0 0 1 1 1 1	1 2 0 ? 1 1 1 1 1
C. fimbriata	1 0 1 0 1 1 0 1 1 1	2 1 2 1 0 0 1 0 1 1	1 2 0 0 1 1 1 1 1
C. panamensis	1 0 1 0 1 1 0 1 1 1	1 1 1 1 0 0 1 0 1 1	1 2 1 1 1 1 ? 1 1
C. querna	1 0 1 0 0 0 0 0 2 1	0 1 1 1 0 0 1 1 1 1	1 2 1 1 1 1 1 1 1
Syacium guineensis	0 1 1 0 0 0 0 0 0 0	1 0 0 0 1 1 0 0 0 0	0 3 0 0 0 1 1 1 2
S. gunteri	0 1 1 0 0 0 1 0 0 0	2 0 0 0 0 1 0 0 0 0	0 3 0 0 0 1 1 1 2
S. latifrons	0 1 1 1 0 0 1 0 0 0	0 0 0 0 1 1 0 0 0 0	0 3 0 0 0 1 ? 1 2
S. longidorsale	0 1 1 0 0 1 0 0 1 0	0 0 0 0 0 ? 0 0 0 0	0 3 0 0 0 1 ? 1 2
S. maculiferum	0 1 1 0 0 0 0 0 0 0	2 0 0 0 1 1 0 0 0 0	0 3 0 0 0 1 ? 1 2
S. micrurum	0 1 1 0 0 0 0 0 0 0	1 0 0 0 1 1 0 0 0 0	0 3 0 0 0 1 1 1 2
S. ovale	0 1 1 0 0 0 0 0 1 0	0 0 0 0 0 1 0 0 0 0	0 3 0 0 0 1 1 1 2
S. papillosum	0 1 1 1 0 0 1 0 0 0	1 0 0 0 1 1 0 0 0 0	0 3 0 0 0 1 1 1 2

The ingroup consisted of 12 species, the four species of *Cyclopsetta* and the eight species of *Syacium*: *Cyclopsetta chittendeni* Bean, 1895; *C. fimbriata* (Goode & Bean, 1885); *C. panamensis* (Steindachner, 1876); *C. querna* (Jordan & Bollman, 1890); *Syacium guineensis* (Bleeker in Günther, 1862); *S. gunteri* Ginsburg, 1933; *S. latifrons* (Jordan & Gilbert, 1882); *S. longidorsale* Murakami & Amaoka, 1992; *S. maculiferum* (Garman, 1899); *S. micrurum* Ranzani, 1842; *S. ovale* (Günther, 1864); *S. papillosum* (Linnaeus, 1758). We recognize all of the above species as valid on the basis of the recent revisions by Khidir *et al.* (2004) for *Cyclopsetta* and by Murakami and Amaoka (1992) for *Syacium*.

Given that *Citharichthys-Etropus-Cyclopsetta-Syacium* was monophyletic according to Hensley and Ahlstrom (1984) and that *Citharichthys-Etropus-Syacium* was monophyletic according to Berendzen and Dimmick (2002), *Citharichthys* and *Etropus* were chosen as outgroups. *Citharichthys* was represented by *C. gilberti* and *C. stigmaeus*, and *Etropus* was represented by *E. crossotus*.

The analysis was performed using the branch and bound and heuristic options (with 100 replicates) of PAUP version 4.0 beta 10 (Swofford, 2003); all characters were unordered; accelerated character optimization (ACCTRAN) was used. The character matrix is shown in table I.

Materials examined

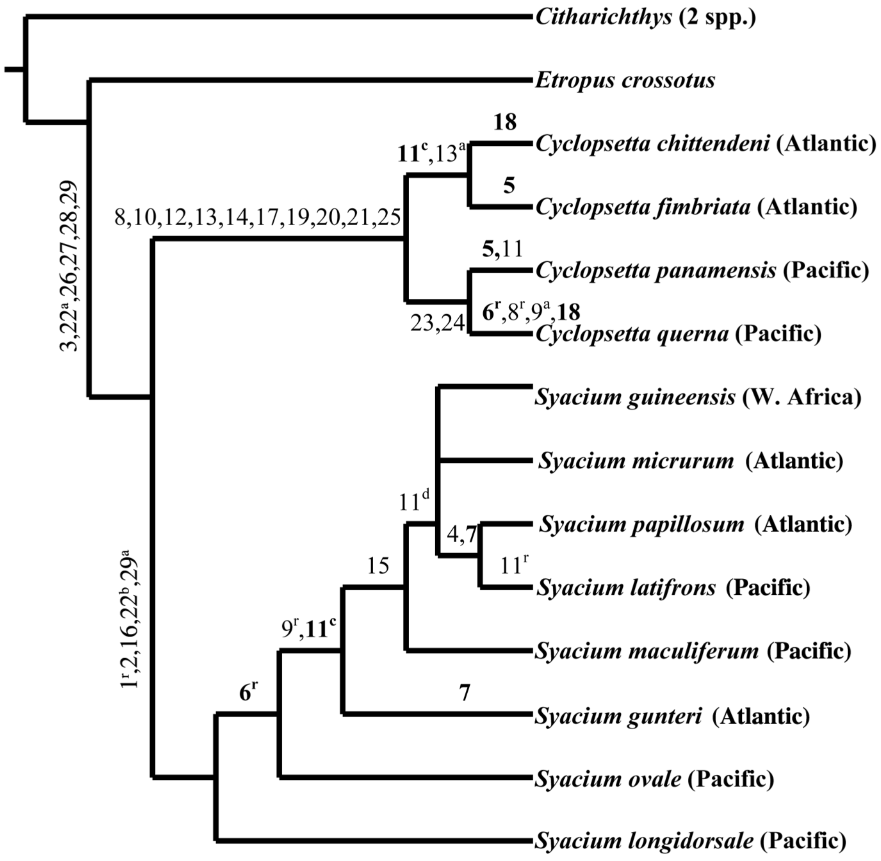
Citharichthys gilberti: NMC 68-1930, Pacific Ocean, Ecuador, 2°52'S-80°7'W, 7 Mar. 1963, 3 ex. (1 c&s), 100-120 mm SL. *C. stigmaeus*: NMC 74-216, Pacific Ocean, California, 33°25'N-118°30'W, 35 m, 23 Jun. 1973, 28 ex. (2 c&s), 62-85 mm SL. *Cyclopsetta*: materials examined are listed in Khidir *et al*. (2004). *Etropus crossotus*: USNM 286059, Atlantic Ocean, Florida, 28°13'30"N-80°21'W, 21.6 m, 14 Nov. 1963, 16 ex. (1 c&s), 13.3-86 mm SL. *Syacium guineensis*: USNM 270657, Atlantic Ocean, Guinea, 9°24'N-15°26'W, 50 m, 29 Nov. 1963, 5 ex. (1 c&s), 171.7-205 mm SL. *S. gunteri*: USNM 266488, Caribbean Sea, Venezuela, 11°25'N-63°49'W, 48.6 m, 24 Sept. 1965, 9 ex. (1 c&s), 99-118 mm SL. *S. micrurum*: USNM 266482, Caribbean Sea, Venezuela, 12°27'N-70°6'W, 72 m, 3 Oct. 1965, 13 ex. (2 c&s), 119.6-190.5 mm SL. *S. papillosum*: USNM 286676, Gulf of Mexico, Florida, 26°24'N-83°22'W, 54 m, 22 Mar. 1966, 7 ex. (2 c&s), 99-159.3 mm SL. *S. longidorsale*: USNM 317827, paratypes, Pacific Ocean, Ecuador, 3°1'N-77°50'W, 35-38 m, 16 Sept. 1966, 15 ex. (2 c&s), 85-120.5 mm SL. *S. ovale*: USNM 317828, Pacific Ocean, Ecuador, 3°1'N-77°50'W, 35-38 m,16 Sept. 1966, 12 ex. (2 c&s), 98.5-168.2 mm SL. *S. maculiferum*: CMNFI 2004-8, Pacific Ocean, Costa Rica, Isla del Coco, 5°33'32" N-87°4'44" W, 3 Apr. 1972, 3 ex. (2 c&s), 98-112 mm SL. *S. latifrons*: CAS 36624, Pacific Ocean, Baja, Mexico, 27 Apr. 1976, 2 ex. (1 c&s), 110.8-118 mm SL.

RESULTS

Branch and bound and heuristic searches resulted in one most parsimonious tree with 48 steps, a consistency index (CI) = 0.75, retention index (RI) = 0.85, and 21 of 29 characters with CI = 1 (Fig. 1, Appendix).

The clade *Cyclopsetta-Syacium* is monophyletic based on six synapomorphies: scaled snout (3), spinulate or serrated gill rakers (22), five haemal parapophyses (26), 5-11 prolonged dorsal fin rays on crest of head in larvae (27), large preopercular spines in larvae (28) and 3-6 elongated rays in the left pelvic fin in larvae (29).

Cyclopsetta is monophyletic with ten synapomorphies: convex interorbital except in *C. querna* where the character reverts to concave (8); posterior margin of lower eye not extending beyond maxillary (10); no notch in front of upper eye (12); origin of dorsal fin between blind side nostrils or anterior to this location (13); three dark lappets along the opercular margin (14); ocelli on the dorsal and anal fins (17); triangle-like lachrymal (19, Fig. 2A); subopercular process with bulbous tip (20, Fig. 3A); quadrate overlapping with the metapterygoid (21, Fig. 4A), and 72-103 lateral line scales (25).



Citharichthys (2 spp.)
Etropus crossotus
$3,22^{a},26,27,28,29$
$8,10,12,13,14,17,19,20,21,25$
18
$\mathbf{11^{c}},13^{a}$
Cyclopsetta chittendeni (Atlantic)
5
Cyclopsetta fimbriata (Atlantic)
5,11
Cyclopsetta panamensis (Pacific)
$\mathbf{6^{r}},8^{r},9^{a},\mathbf{18}$
23,24
Cyclopsetta querna (Pacific)
Syacium guineensis (W. Africa)
Syacium micrurum (Atlantic)
11^{d}
4,**7**
Syacium papillosum (Atlantic)
11^{r}
Syacium latifrons (Pacific)
15
$9^{r},\mathbf{11^{c}}$
Syacium maculiferum (Pacific)
$1^{r},2,16,22^{b},29^{a}$
$\mathbf{6^{r}}$
7
Syacium gunteri (Atlantic)
Syacium ovale (Pacific)
Syacium longidorsale (Pacific)

Figure 1. - Cladogram from an analysis of 29 characters for 12 ingroup species of *Cyclopsetta* and *Syacium* and three outgroup species of *Citharichthys* and *Etropus*. Character change is 0→ 1 except a: 1→ 2, b: 2→ 3, c: 0→ 2, d: 2→1; bold: convergence; r: reversal. *[Cladogramme résultant d'une analyse de 29 caractères pour 12 espèces de* Cyclopsetta *et* Syacium *et trois espèces extra groupes de* Citharichthys *et* Etropus. *Les changements de caractères vont de 0→1 sauf a : 1→2, b : 2→3, c : 0→2, d : 2→1 ; en gras : convergence ; r : réversion.]*

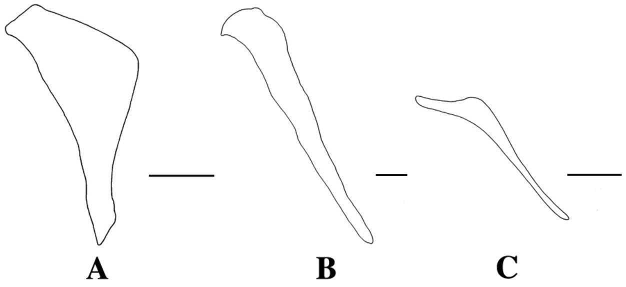


Figure 2. - Lachrymal on ocular side. **A**: *Cyclopsetta chittendeni*, AMNH 81153 (118 mm SL); **B**: *Syacium micrurum*, USNM 266482 (190.5 mm SL); **C**: *Citharichthys stigmaeus*, NMC 74-216 (80 mm SL). Scale bars = 1 mm. *[Os lacrymal de la face oculée. Échelles = 1 mm.]*

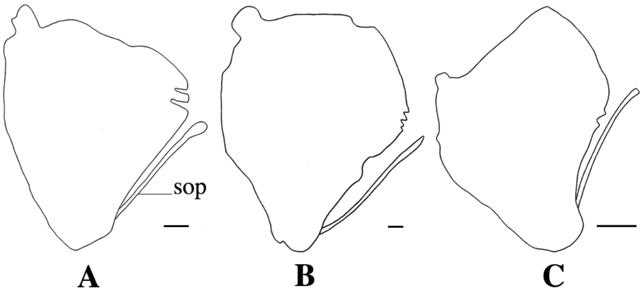


Figure 3. - Suboperculum on ocular side. **A**: *Cyclopsetta panamensis*, USNM 220796 (110 mm SL); **B**: *Syacium micrurum*, USNM 266482 (190.5 mm SL); **C**: *Citharichthys stigmaeus*, NMC 74-216 (80 mm SL). sop = subopercular process. Scale bars = 1 mm. *[Sous-operculaire de la face oculée. sop = processus sous-operculaire. Échelles = 1 mm.]*

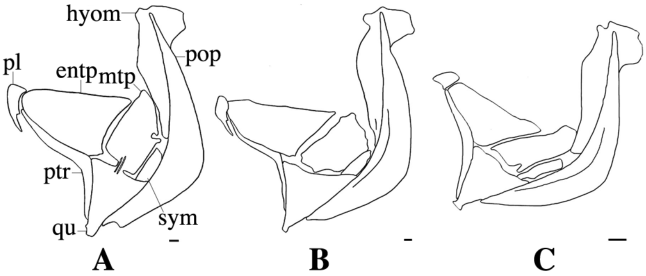


Figure 4. - Suspensorium on ocular side. **A**: *Cyclopsetta chittendeni*, AMNH 81153 (118 mm SL); **B**: *Syacium micrurum*, USNM 266482 (190.5 mm SL); **C**: *Citharichthys stigmaeus*, NMC 74-216 (80 mm SL). entp: entopterygoid; hyom: hyomandibular; mtp: metapterygoid; pl: palatine; pop: preopercle; ptr: pterygoid; qu: quadrate; sym: symplectic. Scale bars = 1 mm. *[Suspensorium de la face oculée. entp: entoptérygoïde; hyom: hyomandibulaire; mtp: métaptérygoïde; pl: os palatin; pop: préopercule; ptr: ptérygoïde; qu: carré; sym: symplectique. Échelles = 1 mm.]*

Cyclopsetta is divided into two clades proposed as the subgenera *Cyclopsetta* and *Azevia*. The subgenus *Cyclopsetta* has two synapomorphies: flap of skin on the ventral side of lower jaw (11), and dorsal fin origin above or advanced relative to anterior blind side nostril (13). It includes *C. fimbriata* with anterior nostril at the same level as posterior (5) and *C. chittendeni* with cycloid scales (18).

The subgenus *Azevia* has two synapomorphies: caudal vertebrae in the range 28-31 (23), and pectoral fin rays in the range 14-18 (24). It includes *C. panamensis* and *C. querna*. *C. panamensis* has two apomorphies: anterior nostril at the same level as the posterior (5), and flap of skin restricted to the posterior angle of the lower jaw (11). *C. querna* has four apomorphies: scaled interorbital space (6), a reversal; concave interorbital (8), a reversal; upper eye slightly advanced relative to lower eye (9), and cycloid scales (18).

The monophyly of *Syacium* is supported by five synapomorphies: two rows of teeth on the upper jaw (1), a reversal; papillae present along entire lips (2); dark bars on pectoral fin (16); short, stout and serrated gill rakers (22); and all six rays of the left pelvic fin elongated in larvae (29).

The cladogram indicates that the ancestor to *Syacium* branched into *S. longidorsale*, with a naked interorbital space, and the ancestor to the remaining species with the interorbital space reverting to scaled (6). This ancestor in turn gave rise to *S. ovale*, with eyes at the same level, and the ancestor to the remaining six species with two synapomorphies: lower eye in advance of the upper (9), a reversal, and flap of skin on the ocular side lower jaw either only on posterior angle or beyond (11). Next, this ancestor branched into *S. gunteri* with no elongation of the pectoral fin rays in mature males and the ancestor to the remaining five species with one or two elongated and filamentous pectoral fin rays in mature males (15). Subsequently, this ancestor gave rise to *S. maculiferum*, and the ancestor to the next four species with a flap of skin restricted to the posterior angle of the lower jaw (11), except for *S. latifrons* where this character is reversed to none. The remaining four species are grouped in a trichotomy of *S. guineensis, S. micrurum* and two sister species *S. latifrons* and *S. papillosum*. These sister species have two synapomorphies: one or two dark lines from upper eye to tip of snout in mature males (4) and a wide interorbital space in mature males (7).

DISCUSSION

Cyclopsetta + *Syacium* remained monophyletic whether *Citharichthys* or *Etropus* was included in the ingroup. This result confirms the pairing of *Cyclopsetta* and *Syacium* as close genera based on larval characters by Ahlstrom *et al.* (1984). In addition, the phylogenetic analysis confirms the monophyly of *Cyclopsetta* based on the shape of gill rakers (Khidir *et al.*, 2004). *Syacium* is monophyletic; this result further supports the taxonomic study of the genus by Murakami and Amaoka (1992) who did not specifically mention that *Syacium* was monophyletic.

The cladogram suggests that the ancestor of *Cyclopsetta* was distributed on the Atlantic and Pacific sides of North and

South America before the formation of the landbridge, which connected the two continents. When the landbridge formed in the late Pliocene, 5.2 million years ago (Briggs, 1974), it separated the populations on the Atlantic side from those on the Pacific side. Speciation followed giving rise to two species on each side of the landbridge; *C. chittendeni* and *C. fimbriata* on the Atlantic side and *C. querna* and *C. panamensis* on the Pacific side.

With respect to *Syacium*, although weakly supported, the cladogram suggests that speciation may have occurred on the Atlantic and Pacific coasts of the Americas before the formation of the landbridge. After the landbridge appeared, four species survived on the Pacific side and three on the Atlantic. In addition, the larvae of the ancestor to the unresolved trichotomy may have been transported with ocean currents to the coast of West Africa where it gave rise to *S. guineensis*.

Repeating the analysis using DNA characters is needed to further test the speciation patterns observed in this study and to resolve the trichotomy within *Syacium*.

Classification

The results of this study indicate that *Cyclopsetta* is monophyletic and divided into two subgenera *Cyclopsetta* and *Azevia*. *Cyclopsetta* is selected as the subgenus of the *C. fimbriata-C. chittendeni* clade because *C. fimbriata* is the type-species of the genus. *Azevia* is selected as the subgenus of the *C. panamensis-C. querna* clade because *Azevia panamensis* Jordan in Jordan & Goss, 1889 was proposed as a new combination for *Cyclopsetta panamensis* (Steindachner, 1876) and is an available name. *Syacium* comprised eight species (Murakami and Amaoka, 1992) and is also monophyletic.

Taxonomic list of *Cyclopsetta* and *Syacium*: an asterisk indicates that the ordering for the species is not clear; *S. latifrons* and *S. papillosum* are sister species.

- Genus *Cyclopsetta*
  - Subgenus *Cyclopsetta*
    - *C. (C.) chittendeni*
    - *C. (C.) fimbriata*
  - Subgenus *Azevia*
    - *C. (A.) panamensis*
    - *C. (A.) querna*
- Genus *Syacium*
  - *S. longidorsale*
  - *S. ovale*
  - *S. gunteri*
  - *S. maculiferum*
  - *S. latifrons**
  - *S. papillosum**
  - *S. micrurum**
  - *S. guineensis**

Acknowledgments. - We thank the following people for loan of specimens and permission to clear and stain some of them: Susan L. Jewett (USNM); Sylvie Laframboise Canadian Museum of Nature (CMN), David Catania (CAS), Damaris Rodriguez (AMNH). William Bussing (UCR) donated three specimens of *Syacium maculiferum* to the CMN; Jennifer Scott (CMN) helped with the figures. This work was supported by a discovery grant to François Chapleau by the National Sciences and Engineering Research Council of Canada.

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Reçu le 23 juillet 2004.
Accepté pour publication le 27 janvier 2005.

APPENDIX

List of characters (note that sexual dimorphism was not observed in species of *Cyclopsetta* or in species used in the outgroups):

Character 1 (CI = 0.50); rows of teeth on upper jaw: two (state 0), one (state 1).

Character 2 (CI = 1.00); lip papillae: absent (state 0), present along entire lips (state 1), present only along front of lips (state 2).

Character 3 (CI = 1.00); scales on snout: absent (state 0), present (state 1).

Character 4 (CI = 1.00); one or two dark lines from the anterior margin of upper eye to tip of snout in mature males: absent (state 0); present (state 1).

Character 5 (CI = 0.50); position of anterior nostril relative to posterior nostril (Fig. 3 in Khidir *et al*., 2004): dorsal (state 0), same level (state 1).

Character 6 (CI = 0.33); scales in interorbital space: present (state 0), absent (state 1).

Character 7 (CI = 0.50); width of interorbital space in mature males relative to that in females: similar (state 0), much wider (state 1).

Character 8 (CI = 0.33); shape of interorbital bone: concave (state 0), convex (state 1).

Character 9 (CI = 0.67); upper eye position relative to lower eye: lower eye advanced (state 0), both eyes at same level (state 1), upper eye slightly advanced (state 2).

Character 10 (CI = 1.00); lower eye position relative to maxillary: only posterior margin of lower eye extending beyond maxillary (state 0), posterior margin of lower eye not extending beyond maxillary (state 1), all of lower eye extending beyond maxillary (state 2).

Character 11 (CI = 0.40); flap of skin on ventral aspect of ocular side lower jaw (Fig. 3 in Khidir *et al*., 2004): absent (state 0), present only on posterior angle (state 1), present beyond posterior angle (state 2).

Character 12 (CI = 1.00); notch in front of upper eye: present (state 0), absent (state 1).

Character 13 (CI = 1.00); origin of dorsal fin relative to blind side nostrils (Fig. 2 in Khidir *et al*., 2004): behind posterior nostril (state 0), between nostrils (state 1), above or advanced relative to anterior nostril (state 2).

Character 14 (CI = 1.00); lappets along opercular margin: not present but replaced by a continuous ribbon-like flap of skin (state 0), three dark lappets (state 1).

Character 15 (CI = 1.00); first one or two pectoral fin rays extended and filamentous in mature males: absent (state 0), present (state 1).

Character 16 (CI = 1.00); dark bars on pectoral fin : absent (state 0), present (state 1).

Character 17 (CI = 1.00); ocelli on dorsal and anal fins: absent (state 0); present (state 1).

Character 18 (CI = 0.50); type of scales: ctenoid (state 0), cycloid (state 1).

Character 19 (CI = 1.00); shape of lachrymal: elongated (state 0, Fig. 2b and c), triangle-like (state 1, Fig. 2a).

Character 20 (CI = 1.00); shape of subopercular process: straight (state 0, Fig. 3b and c), with bulbous tip (state 1, Fig. 3a).

Character 21 (CI = 1.00); quadrate overlapping with metapterygoid: absent (state 0, Fig. 4b and c), present (state 1, Fig. 4a).

Character 22 (CI = 1.00); shape of gill rakers on first gill arch (Fig. 1 in Khidir *et al*., 2004): long and slender (state 0), short and stout (state 1), short broad and spinulate (state 2), short stout and serrated (state 3).

Character 23 (CI = 1.00); number of caudal vertebrae: 24-27 (state 0), 28-31 (state 1).

Character 24 (CI = 1.00); number of pectoral fin rays: 10-13 (state 0), 14-18 (state 1).

Character 25 (CI = 1.00); number of lateral line scales: 40-69 (state 0), 72-103 (state 1).

Character 26 (CI = 1.00); number of abdominal vertebrae with haemal parapophyses: six (state 0), five (state 1).

Character 27 (CI = 1.00); number of prolonged dorsal fin rays on crest of head in larvae: 0-3 (state 0), 5-11 (state 1).

Character 28 (CI = 1.00); preopercular spines in larvae: small (state 0), large (state 1).

Character 29 (CI = 1.00); elongated rays of left pelvic fin in larvae: 0-2 (state 0), three (state 1), all six (state 2).